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Growth and development of copepodite stages of *Pseudocalanus* spp.

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Quantitative expressions are presented describing the effects of temperature and food concentration on the growth and development of the copepodite stages of Pseudocalanus spp. The calculations were made on the basis of experimental data from the literature for two geographically separate populations of Pseudocalanus from Puget Sound (Washington, USA) and from the southern North Sea. Relationships were obtained between the growth parameters for Pseudocalanus sp. from Puget Sound and temperature in the 8–15.5°C range and food concentrations from 10 mg C m^{-3} to excess, as well as for Pseudocalanus elongatus from the southern North Sea at high food concentrations and in the 4–15°C temperature range. Also computed was the total development time of P. elongatus for the final four copepodid stages as a function of food concentration from 50 mg C m^{-3} to excess and temperature from 5 to 20°C. Empirical models computed here may be used with good precision in mathematical models of pelagic communities.

INTRODUCTION

Mathematical models of pelagic communities, particularly of the lower trophic levels represented by plankton, require detailed descriptions of the various relationships between the rates of physiological processes of the dominant species and environmental factors. The literature provides ample experimental data on these factors for several species of zooplankton. This information can be applied to gain some idea of the functional relationships potentially useful in simulating the response of zooplankton to variations in their environment. The elaboration of such theoretical descriptions is critical to the inclusion of these animals, as animals, in more general simulations of ecosystems. Planktonic copepods (*Pseudocalanus*, *Temora*, *Acartia*) are important components of the diet of numerous species of fish in the North Sea and adjacent waters, e.g. in the Baltic Sea and the English Channel, as well as in Puget Sound, Nova Scotia and Canadian Arctic waters. In all of these waters, the copepod *Pseudocalanus* is one of the more abundant zooplankton species.

Experiments on the growth rate of the copepodid stages of *Pseudocalanus* spp. suggest that this parameter is directly proportional to food concentration (Paffenhöfer and Harris, 1976; Corkett and McLaren, 1978; Vidal, 1980a; Klein Breteler *et al.*, 1995) and that it is strongly influenced by food quality (Koski *et al.*, 1998). The development of *Pseudocalanus* spp. has also been found to accelerate with temperature (McLaren, 1965; Vidal, 1980a; Thompson, 1982; Klein Breteler *et al.*, 1995). However, the combined effect of food concentration and temperature as a function of these two parameters on growth has not been established for *Pseudocalanus* spp. This is a key statement, since it is the motivation and justification for the present study. While equation (19) in Vidal's paper (Vidal, 1980a) did describe such a dependence for *Calanus pacificus*, his data were insufficient to do likewise for *Pseudocalanus*.

The present work advances the idea of establishing the combined effect of temperature and food concentration on the growth and development of the copepodid stages of *Pseudocalanus* sp. It is important to investigate and identify the critical factors in mathematical models of pelagic communities with a high-resolution zooplankton module, since as a top-down regulator, zooplankton may play a significant role in marine ecosystems.

METHOD

The present analysis is based on literature data. These, in turn, were obtained on the basis of materials collected in Puget Sound, Washington, USA (Vidal, 1980a) and from the North Sea (Thompson, 1982; Klein Breteler

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et al., 1995). *Pseudocalanus* sp. from Puget Sound were collected with a plankton net (215 μm mesh size) hauled through the upper 30 m. Starting with stages CI or CII, the copepodid stages were cultured at 15.5, 12 and 8°C. The food source in all these experiments was the single-cell, pillbox-shaped centric diatom *Thalassiosira eccentrica*, isolated from the main basin of Puget Sound. *Thalassiosira eccentrica* (Ø = 20 μm) provided 100% of the food at 15.5 and 8°C, and 50% at 12°C, while the other 50% at 12°C consisted of *T. eccentrica* (Ø = 34 μm). Cell sizes, carbon contents and the concentrations of diatoms used in the experiments are shown in table 1 in Vidal (Vidal, 1980a), where 1 p.p.m. (food concentration) = 92 mg C m^{-3} for *T. eccentrica* (Ø = 20 μm) and 1 p.p.m. = 72 mg C m^{-3} for *T. eccentrica* (Ø = 34 μm).

Pseudocalanus elongatus from the North Sea (Thompson, 1982) were collected with supplies of live plankton using a standard Fine International Net of 61 μm mesh. The temperature of the cultures was kept at 4–15°C. All stages were fed with *Isochrysis galbana* at a concentration of 300 000 cells ml^{-1}. Klein Breteler *et al.*, on the other hand, bred the pelagic copepod *P. elongatus* three times from stage I and II nauplii at 5, 10, 15 and 20°C, and with four different rations of the autotrophic algae *Rhodomonas* sp. and *I. galbana*, and the heterotrophic dinoflagellate *Oxyrrhis marina* as food (Klein Breteler *et al.*, 1995).

A detailed description of the culture techniques used for *Pseudocalanus* from Puget Sound can be found in Vidal (Vidal, 1980a); similarly, those used for *Pseudocalanus* from the North Sea can be found in Thompson (Thompson, 1982) and Klein Breteler *et al.* (Klein Breteler *et al.*, 1995).

In the present work, the relationships between the results from these three papers and temperature and food concentrations were found by performing linear regression following appropriate transformation of these data.

Growth rate

Natural phytoplankton provide a wide selection of possible sizes of food items. Nevertheless, as in these, and nearly all other experiments, a first approximation is to assume that all sizes of copepods are feeding on the total population, *Phyt*, defined in biomass units such as mg C m^{-3}.

Three of a large number of functions can be used to define the growth rate, g:

$$g = \begin{cases} g_{\max}\dfrac{Phyt - Phyt_0}{k_{Phyt}} & \text{for } Phyt_0 \le Phyt < Phyt_0 + k_{Phyt} \\ g_{\max} & \text{for } \{Phyt\} \ge Phyt_0 + k_{Phyt} \end{cases} \qquad (1)$$

$$g = g_{\max}\left\{1 - \exp\left(\frac{-(Phyt - Phyt_0)}{k_{Phyt}}\right)\right\} \qquad (2)$$

$$g = g_{\max}\frac{Phyt - Phyt_0}{k_{Phyt} + Phyt - Phyt_0} \qquad (3)$$

where $g_{\max}$ (% of weight day^{-1}) is the maximum growth rate, *Phyt* (mg C m^{-3}) is the food concentration, $Phyt_0$ (mg C m^{-3}) is the value of *Phyt* at which $g = 0$ and k_{Phyt} (mg C m^{-3}) is the ingestion rate, since $g_{\max}/k_{Phyt}$ for *Phyt* is slightly greater than $Phyt_0$. In all three, $g = 0$ when $Phyt \le Phyt_0$. Each relationship depends on three constants and satisfies the same three conditions:

1. $g = 0$ when $Phyt = Phyt_0$
2. $g = g_{\max}\dfrac{Phyt - Phyt_0}{k_{Phyt}}$ for *Phyt* slightly greater than $Phyt_0$
3. $g \to g_{\max}$ as $Phyt \to \infty$

These correspond to three results of experimental studies of growth: (1) there may or may not be a threshold, $Phyt_0$, below which the animals do not grow; (2) when feeding starts, the growth rate increases in proportion to the rise in food concentration; (3) as food concentration approaches high values, the growth rate tends to become constant.

Pseudocalanus from Puget Sound, Washington

This subsection describes growth rates of *Pseudocalanus* sp. for developmental stages CII–CV using equation (2), which corresponds to equation (3) used by Vidal (Vidal, 1980a), where food concentration is expressed in p.p.m. The developmental stages of *Pseudocalanus* sp. were defined by their mean body weight [see figure 1 in Vidal (Vidal, 1980a)]. The values of the parameters in equation (2) as a function of food concentration, *Phyt*, were taken according to Vidal's data (Vidal, 1980a) on the assumption that $k_{Phyt} = \delta^{-1} fc$, where δ is the slope of the growth curve given in Vidal (Vidal, 1980a) and *fc* is the parameter converting food concentration to different units, i.e. to mg C m^{-3} [fc = 92 mg C m^{-3} at 15.5 and 8°C, but fc = 72 mg C m^{-3} at 12°C; see table I in Vidal (Vidal, 1980a)]. These values are given in Table I as $g^{V}{}_{\max} = f(Phyt)$, $k^{V}{}_{Phyt} = f(Phyt)$ and $Phyt_0 = f(Phyt) = 0$.

Transformation of these data (see Table I, columns 3 and 4) to a base 10 logarithm gives a linear relationship between temperature and $g_{\max}$ as well as between temperature and k_{Phyt}. The parameters $g_{\max}$ and k_{Phyt} as a function of food concentration increase with increasing

Table I: Parameters g_{max}, k_{Phyt} and $Phyt_c$ of the growth model of Pseudocalanus sp. for developmental stages CII–CV

Stage	Temperature (°C)	$g^V_{max} = f(Phyt)$	$k^V_{Phyt} = f(Phyt)$	$g^V_{max} = f(Phyt.\ T)$	$k_{Phyt} = f(Phyt.\ T)$	$Phyt_c = f(Phyt.\ T)$	$g^T_{max} = f(Phyt.\ T)$
CII	15.5	25.75	60.77	26.45	58.11	140.1	29.65
	12.0	22.63	35.5	21.63	38.21	91.95	24.38
	8.0	15.55	20.23	15.82	19.67	46.6	17.86
CIII	15.5	25.36	60.65	25.68	61.40	148.0	18.78
	12.0	21.60	40.76	41.17	40.15	95.7	22.76
	8.0	15.49	20.09	15.62	20.25	48.0	15.74
CIV	15.5	24.10	60.33	24.50	69.78	168.3	21.39
	12.0	21.05	56.40	20.51	44.43	106.5	17.83
	8.0	15.31	19.83	15.48	21.75	51.5	13.38
CV	15.5	17.46	72.50	17.64	97.75	234.9	15.14
	12.0	16.21	87.80	15.93	54.29	130.0	12.67
	8.0	13.41	17.84	13.52	21.48	50.9	9.54

g^V_{max} and k^V_{Phyt} according to Vidal (Vidal, 1980a); g^T_{max} was obtained in this paper for *P. elongatus*Th after Thompson (Thompson, 1982), where g_{max} is the maximum growth rate (in % of weight day^{-1}), k_{Phyt} is the ingestion rate as g_{max}/k_{Phyt} for *Phyt* slightly greater than $Phyt_0$ (in mg C m^{-3}) and $Phyt_c$ is the critical food concentration (in mg C m^{-3}).

temperature (Figure 1). These relationships are described by the equations:

$$\log g_{max} = a + b \log T \tag{4}$$

$$\log k_{Phyt} = a + b \log T \tag{5}$$

The values of *a*, *b* and *r*, and the correlation coefficient for developmental stages CII–CV are given in Table II.

The values of g_{max} and k_{Phyt} computed with equations (4) and (5) as a function of temperature (Table II) and the values of $Phyt_c$ copepodids of *Pseudocalanus* sp. are given in Table I [as $g_{max}=f(Phyt, T)$, $k_{Phyt}=f(Phyt, T)$ and $Phyt_c = f(Phyt, T)$] together with the values given by Vidal (Vidal, 1980a). The parameter $Phyt_c$ is the critical food concentration, which is arbitrarily defined as the value of *Phyt* at which g = 90% of g_{max}, calculated using equation (2). Ninety-six per cent of the value of g_{max} computed with equation (4) and 83% of the value of k_{Phyt} computed with equation (5) as a function of temperature lie within the range of the parameters given by Vidal (Vidal, 1980a). Thus, by substituting g_{max} and k_{Phyt} in equation (2) for equations (4) and (5) (Table II), equation (2) can be used to describe the growth rate of *Pseudocalanus* sp. for developmental stages CII–CV as a function of both food concentration and temperature:

$$\text{For CII } g = 3.141 \times 10^{0.777 \log T} \left(1 - e^{-Phyt/0.656 \times 10^{1.636 \log T}}\right) \tag{6}$$

$$\text{For CIII } g = 3.266 \times 10^{0.752 \log T} \left(1 - e^{-Phyt/0.616 \times 10^{1.677 \log T}}\right) \tag{7}$$

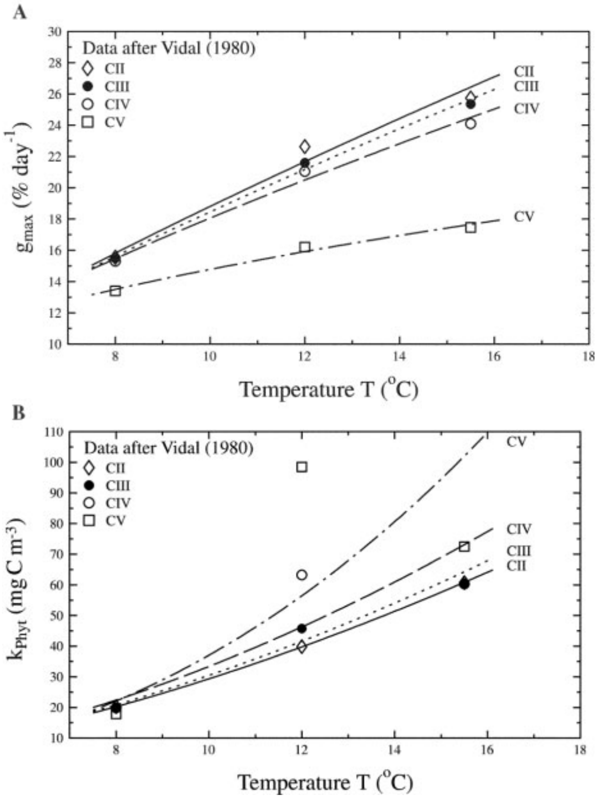

Fig. 1. Relationship between the parameters of equation (2), g_{max} and k_{Phyt}, and temperature T (in °C) for developmental stages CII–CV of *Pseudocalanus* sp., where g_{max} is the maximum growth rate (in % of weight day^{-1}) and k_{Phyt} is the ingestion rate as g_{max}/k_{Phyt} for *Phyt* slightly greater than $Phyt_0$ (in mg C m^{-3}).

Table II: Equations describing the relationship between parameters of equation (2), g_{max} and k_{Phyt}, and temperature T (in °C) for developmental stages CII–CV of Pseudocalanus sp. and P. elongatusTh

Equation	Stage	a	b	r
Pseudocalanus sp.				
$\log g_{max} = a + b \log T$	CII	0.497	0.777	0.989
	CIII	0.514	0.752	0.998
	CIV	0.562	0.695	0.995
	CV	0.765	0.405	0.993
$\log k_{Phyt} = a + b \log T$	CII	−0.183	1.636	0.993
	CIII	−0.208	1.677	0.999
	CIV	−0.255	1.763	0.943
	CV	−0.731	2.284	0.876
P. elongatusTh				
$\log g_{max} = a + b \log T$	CII	0.558	0.768	0.993
	CIII	0.375	0.910	0.949
	CIV	0.488	0.707	0.849
	CV	0.350	0.697	0.937

g_{max} is the maximum growth rate (in % of weight day^{-1}) and k_{Phyt} is the ingestion rate as g_{max}/k_{Phyt} for *Phyt* slightly greater than $Phyt_0$ (in mg C m^{-3}).

$$\text{For CIV } g = 3.648 \times 10^{0.695 \log T} \left(1 - e^{-Phyt/0.556 \times 10^{1.763 \log T}}\right) \quad (8)$$

$$\textit{For CV } g = 5.821 \times 10^{0.404 \log T} \left(1 - e^{-Phyt/0.186 \times 10^{2.284 \log T}}\right) \quad (9)$$

assuming that the food concentration ($Phyt_0$) at which $g = 0$ was zero.

Pseudocalanus from the southern North Sea

Thompson determined the stage duration of *P. elongatus*Th [this abbreviation meant *P. elongatus* from the North Sea after Thompson (Thompson, 1982)] at temperatures ranging from 4 to 15°C on the basis of laboratory experiments (Thompson, 1982). The development times obtained by Thompson were probably not limited by food availability, and it can be assumed that they are close to the maximum rates. According to these data, the maximum growth rates of *P. elongatus*Th for stages CII–CV were obtained by the numerical solution of polynomials of the appropriate degrees. The polynomials at the given temperature were described by:

$$(W_i + W_i g_{max})(1 + g_{max} + g_{max}^2 + ... + g_{max}^{n-1} + g_{max}^d) = W_{i+1}$$

where W_i is the mean body weight for successive copepodid stages, $n + d$ is the stage duration (e.g. when D = 5.36 days, n = 5 and d = 0.36) and g_{max} is an unknown quantity. Transformation of these data to a base 10 logarithm gives a linear relationship between temperature and the value of g_{max} at that temperature, $g^T{}_{max}$, i.e. $\log g_{max} = a + b \log T$. The values of a, b and r, and the correlation coefficient for each developmental stage are given in Table II. Figure 2 shows a plot of the maximum growth rate for each stage against temperature.

Stage duration

The maximum growth rate, g_{max}, of *Pseudocalanus* sp. for stages CII–CV computed with the equations given in Table II was used to express numerically the minimum stage duration, D_{min}. D_{min} is the minimum value for which the development rates were not limited by food

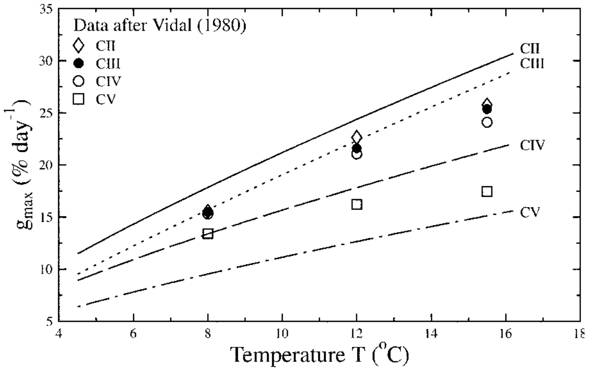

Fig. 2. Relationship between the maximum growth rate g_{max} (in % of weight day^{-1}) and temperature T (in °C) for developmental stages CII–CV of *P. elongatus*Th.

availability. The common logarithm of $D_{\min}$ for *Pseudocalanus* sp. as well as *P. elongatus*Th was related linearly to the common logarithm of temperature:

$$\log D_{\min} = a + b \log T \qquad (10)$$

The values of a, b and r, and the correlation coefficient for stages CII–CV are given in Table III. The regression equations for each stage from CII to CV of *Pseudocalanus* sp. at temperatures ranging from 8 to 15.5°C and for *P. elongatus*Th at temperatures ranging from 4 to 15°C are shown in Figure 3.

The stage duration, D, of *Pseudocalanus* sp. for copepodid stages at the different food concentrations was also obtained here. The growth rates of *Pseudocalanus* sp. for stages CII–CV (defined by their mean body weights) computed with equations (6)–(9) were used to obtain the stage duration by the numerical solution of polynomials of unknown degrees (see the previous subsection). The stage duration, D, of *Pseudocalanus* sp. was found to be very sensitive to changes in temperature and food concentration. Transformation of these data for D to natural logarithms gave a linear relationship between time and food concentration. This relationship was described with the equation:

$$\ln (D - D_{\min}) = a + bPhyt \qquad (11)$$

The values of a, b and r, and the correlation coefficient for each developmental stage CII–CV and for the total period of growth from CII to CV at temperatures ranging from 8 to 15°C are given in Table IV.

The coefficients a and b of the equations describing D as a function of food concentration were obtained as a function of temperature by means of a linear–log and an exp–linear regression on the data for coefficients a and b, respectively. The regression equations for each stage together with the correlation coefficients are given in Table V.

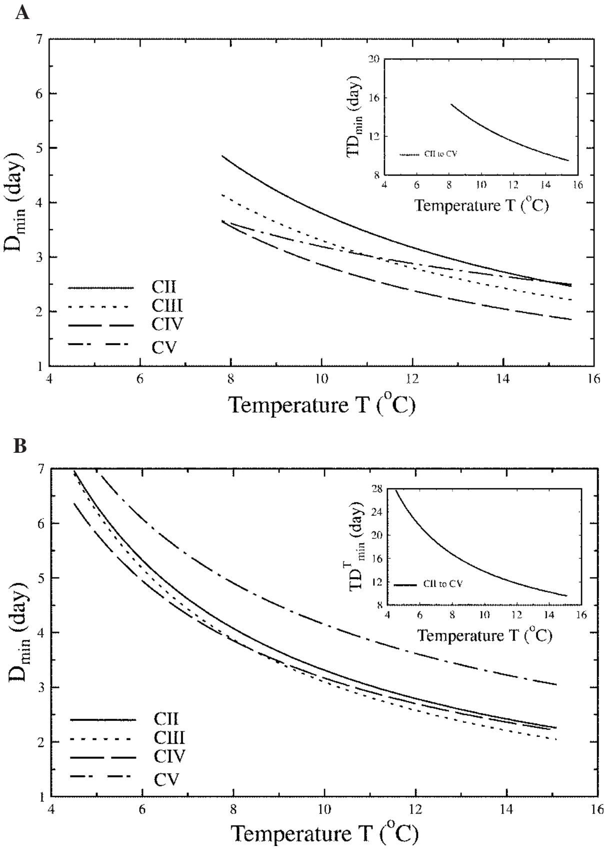

Fig. 3. Relationship between the minimum stage duration $D_{\min}$ (in days) and temperature T (in °C) for developmental stages CII–CV of *Pseudocalanus* sp. (**A**) and *P. elongatus*Th (**B**), where $TD_{\min}$ is the total duration (in days).

Table III: Equations describing the relationship between the minimum stage duration D_{min} (in days) and temperature T (in °C) for developmental stages CII–CV of Pseudocalanus sp. and P. elongatusTh

Equation	Stage	*a*	*b*	*r*
Pseudocalanus sp.	CII	1.57	−0.988	−0.989
log $D_{\min}$ = a + b log T	CIII	1.43	−0.911	−0.996
	CIV	1.44	−0.987	−0.957
	CV	1.06	−0.559	−0.994
	CII–CV	1.98	−0.860	−0.989
P. elongatusTh	CII	1.45	−0.931	−0.989
log $D_{\min}$ = a + b log T	CIII	1.49	−1.004	−0.956
	CIV	1.37	−0.873	−0.902
	CV	1.37	−0.749	−0.941
	CII–CV	2.02	−0.879	−0.992

Table IV: The coefficients a and b of equation (11) describing the stage duration D (in days) as a function of food concentration Phyt (in mg C m^{-3}) for developmental stages CII–CV of Pseudocalanus sp.

Stage	Temperature	*a*	*b*	*r*
CII	8.6	1.64	−0.0342	−0.959
	9.7	1.54	−0.0284	−0.935
	10.8	2.03	−0.0346	−0.986
	12.6	2.06	−0.0295	−0.979
	14.5	2.26	−0.0256	−0.983
CIII	8.6	1.45	−0.0333	−0.957
	9.7	1.77	−0.0339	−0.979
	10.8	1.50	−0.0293	−0.937
	12.6	2.14	−0.0289	−0.989
	14.5	2.19	−0.0245	−0.981
CIV	8.6	1.40	−0.0328	−0.961
	9.7	1.73	−0.0335	−0.980
	10.8	1.81	−0.0350	−0.977
	12.6	1.98	−0.0287	−0.984
	14.5	2.11	−0.0259	−0.979
CV	8.6	1.56	−0.0331	−0.969
	9.7	2.04	−0.0346	−0.988
	10.8	2.15	−0.0298	−0.980
	12.6	2.29	−0.0203	−0.950
	14.5	2.59	−0.0190	−0.949
Total	8.6	2.99	−0.0393	−0.994
CII–CV	9.7	2.62	−0.0179	−0.790
	10.8	3.19	−0.0320	−0.942
	12.6	3.17	−0.0172	−0.880
	14.5	3.65	−0.0221	−0.967

By substituting *a* and *b* in equation (11) for the equations in Table V, *D* for stages CII to CV of *Pseudocalanus* sp. becomes a function of both food concentration and temperature in the 8–15.5°C range:

$$\text{For CII} \quad D = 36.98 \times 10^{-0.988 \log T} + e^{-1.29 + 3.07 \log T + \ln(0.958 + 0.001124T)\mathit{Phyt}} \tag{12}$$

$$\text{For CIII} \quad D = 29.92 \times 10^{-0.911 \log T} + e^{-1.63 + 3.30 \log T + \ln(0.954 + 0.001483T)\mathit{Phyt}} \tag{13}$$

$$\text{For CIV} \quad D = 27.73 \times 10^{-0.987 \log T} + e^{-1.19 + 2.87 \log T + \ln(0.954 + 0.001319T)\mathit{Phyt}} \tag{14}$$

$$\text{For CV} \quad D = 11.56 \times 10^{-0.559 \log T} + e^{-2.02 + 3.98 \log T + \ln(0.941 + 0.002832T)\mathit{Phyt}} \tag{15}$$

$$\text{Total CII–CV} \quad TD = 99.50 \times 10^{-0.860 \log T} + e^{0.58 + 2.53 \log T + \ln(0.934 + 0.003362T)\mathit{Phyt}} \tag{16}$$

The sets of stage duration curves computed with equations (12)–(15) of *Pseudocalanus* sp. for developmental stages CII–CV are shown in Figure 4.

Klein Breteler *et al.* determined the generation time of *P. elongatus*^{KB} [this abbreviation meant *P. elongatus* from the North Sea after Klein Breteler *et al.* (Klein Breteler *et al.*, 1995)] as a function of temperature for four different food supplies from the rate of development measured in the laboratory (Klein Breteler *et al.*, 1995). In accordance with these data [see table II in Klein Breteler *et al.* (Klein Breteler *et al.*, 1995)], the total stage duration for the final four copepodid stages as a function of food concentration and temperature was obtained in the present work. Transformation of these data yields a linear relationship between the logarithm of food concentration and the total duration, *TD*, of the life cycle stages from CII to CV for each temperature:

$$TD = a - b \log \mathit{Phyt} \tag{17}$$

Table VI sets out the values of *a*, *b* and *r*, and the correlation coefficient for temperatures 5, 10, 15 and

Table V: The coefficients a and b of equations (12–16) describing the stage duration D (in days) as a function of temperature T (in °C) for developmental stages CII–CV of Pseudocalanus sp.

Stage	Coefficient $a = a_1 + b_1 \log T$	r
CII	$a = -1.29 + 3.07 \log T$	0.917
CIII	$a = -1.63 + 3.30 \log T$	0.863
CIV	$a = -1.19 + 2.87 \log T$	0.965
CV	$a = -2.02 + 3.98 \log T$	0.957
Total	$a = 0.58 + 2.53 \log T$	0.872
Stage	Coefficient $e^b = a_2 + b_2 T$	r
CII	$e^b = 0.958 + 0.001124\ T$	0.730
CIII	$e^b = 0.954 + 0.001483\ T$	0.948
CIV	$e^b = 0.954 + 0.001319\ T$	0.850
CV	$e^b = 0.941 + 0.002832\ T$	0.945
Total	$e^b = 0.934 + 0.003362\ T$	0.867

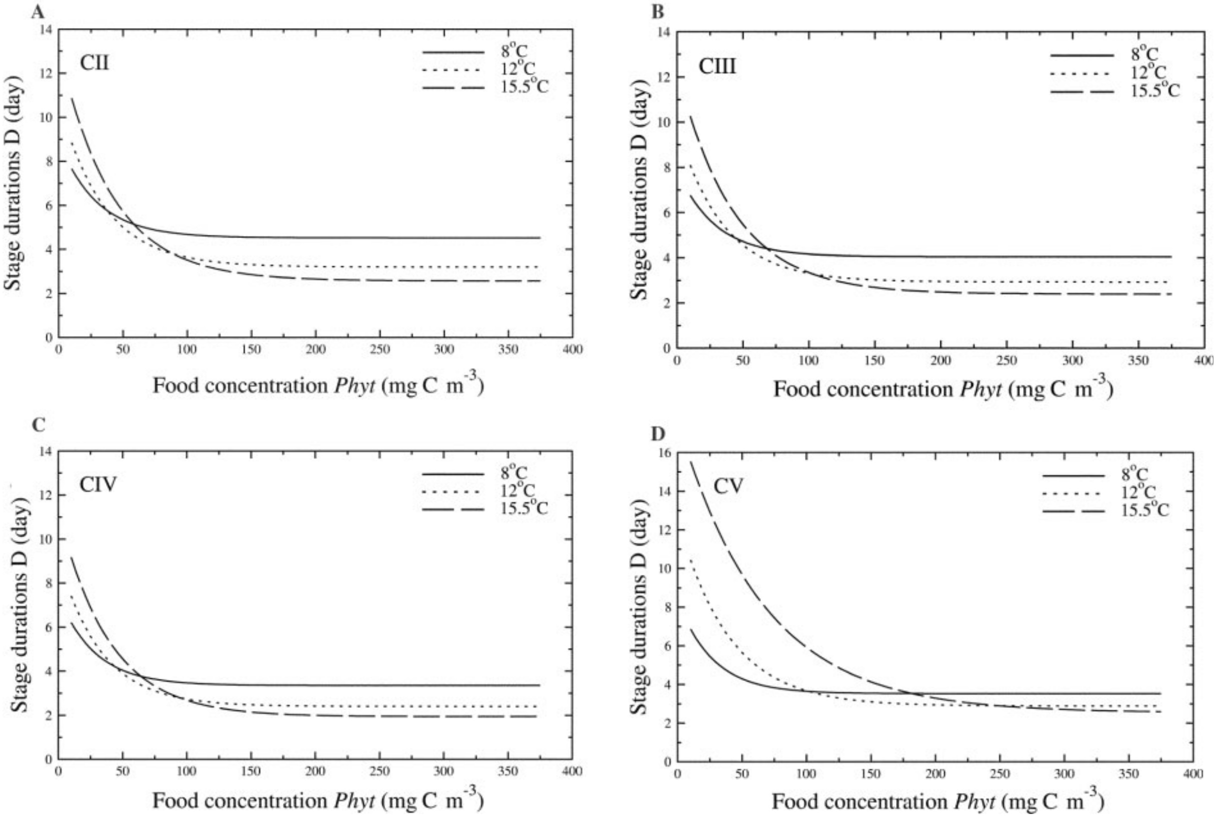

Fig. 4. Relationship between the stage duration *D* (in days) and food concentration *Phyt* (in mg C m^{-3}) for developmental stages CII–CV of *Pseudocalanus* sp.

20°C. The food concentration used in the calculations here is the mean total biomass of food suitable as a food supply [see table I in Klein Breteler *et al.* (Klein Breteler *et al.*, 1995)]. Regression equations for each temperature were obtained for each range of food concentration, and are shown in Figure 5 together with the experimental results. Eighty-three per cent of the value of *TD* computed with equation (17) as a function of food

Table VI: The coefficients a and b of equation (17) describing the total duration TD (in days) and food concentration Phyt (in mg C m^{-3}) for stages from CII to CV of P. elongatus^{KB} at 5, 10, 15 and 20°C

Temperature (°C)	*a*	*b*	*r*
5	44.47	9.07	−0.850
10	24.37	5.72	−0.951
15	27.51	8.63	−0.855
20	15.35	3.16	−0.589

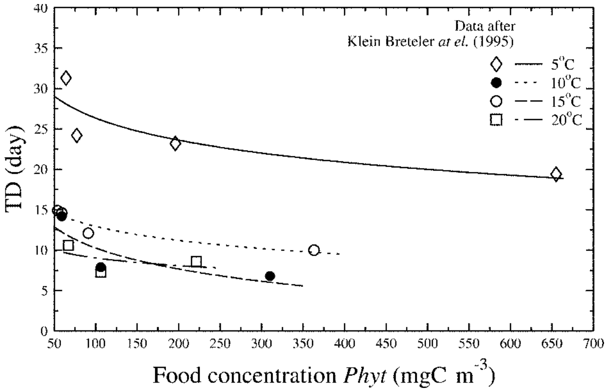

Fig. 5. Relationship between the total duration *TD* (in days) and food concentration *Phyt* (in mg C m^{-3}) for *P. elongatus*^{KB}.

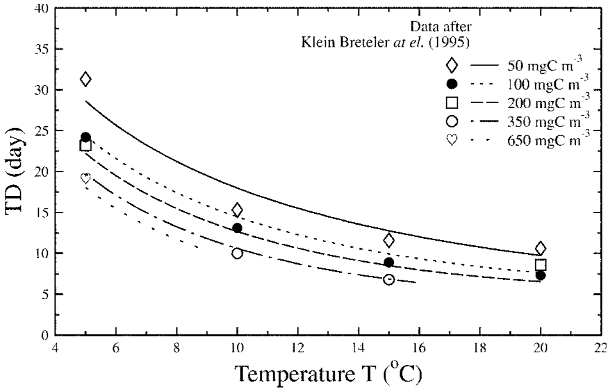

Fig. 6. Relationship between the total duration *TD* (in days) and temperature *T* (in °C) for *P. elongatus*^{KB}.

concentration lies within the range of the parameter *TD* given by Klein Breteler *et al.* (Klein Breteler *et al.*, 1995).

The coefficients *a* and *b* of the food-dependent relationships (Table VI) can be expressed as a function of temperature to yield a single equation incorporating all the variables under study. Although this approach provides little new insight into patterns of development, a general model that includes food concentration and temperature does have considerably greater predictive value. The coefficients *a* and *b* of the equations describing *TD* as a function of food concentration were related to temperature:

$$a = 73.04 - 43.215 \log T, r = -0.927 \qquad (18)$$

$$\log b = 1.087 - 0.0239T, r = -0.728 \qquad (19)$$

By substituting *a* and *b* in equation (17) for equations (18) and (19), *TD* becomes a function of both food concentration and temperature:

$$TD = 73.04 - 43.215 \log T - 10^{1.087-0.0239T} \log Phyt \qquad (20)$$

Values of *TD* for stages CII–CV of *P. elongatus*^{KB} computed with equation (20) for different temperature and food conditions are shown in Figure 6.

RESULTS

Growth rate

The computed maximum growth rate of *Pseudocalanus* sp., g_{max}, decreased with increasing developmental stages. g_{max} for the small stages was sensitive to changes in temperature, but for the larger ones g_{max} became less dependent on temperature. However, the parameter k_{Phyt} for the largest copepodids was very sensitive to changes in temperature, but with decreasing stage of development k_{Phyt} became less dependent on temperature.

The results indicate that the maximum growth rate for copepodids of *Pseudocalanus* sp. obtained in this work as a function of food concentration and temperature is similar to that given by Vidal (Vidal, 1980a) at all temperatures (see Table I, columns 3 and 5). However, the computed value of k_{Phyt} differs slightly from the data given by Vidal (Vidal, 1980a) for the small stages (CII and CIII) at all temperatures. For the larger stages, this difference is greater, i.e. for stage CIV it is ~10% and for stage CV it is ~30% at 12 and 15.5°C. These differences in k_{Phyt} described above were not due to conversion to different units, but rather to the original values of δ (where δ is the slope of the growth curve). In the present paper, it is shown that k_{Phyt} increased with increasing temperature; hence, δ was inversely related to temperature. This conforms to the experimental results given by Vidal (Vidal, 1980a) (see table V in that paper), except in the case when, for the large stages CIV and CV, δ was lower at 12°C than at 15.5°C. The critical food concentration for the growth of *Pseudocalanus* sp., $Phyt_c$, increased with temperature and developmental stage. This trend is particularly evident when data for the extreme temperatures are compared (Table I).

The increase in $g_{\max}$ of *P. elongatus*Th with increasing temperature and decreasing developmental stage is evident from the data given in Table I and Figure 2. The value of $g_{\max}$ for the small stage CII was around twice as high as that for the larger CV. On the basis of the findings in this study and analyses, differences in $g_{\max}$ were found between the two species. For the small stages CII and CIII, $g_{\max}$ of *Pseudocalanus* from the North Sea was higher than that for *Pseudocalanus* from Puget Sound in the 8–15.5°C range, but for the larger CIV and CV it was lower (Table I; Figure 2). The decrease in $g_{\max}$ of *Pseudocalanus* sp. with increasing stage of development was slight for stages CII, CIII and CIV, but for the largest stage CV, this decrease was explicit at all temperatures. In the present work, the calculated $g_{\max}$ of development stages CII–CV for these two species ranged from 26.45 to 17.64% body weight day^{-1} at 15.5°C and from 15.82 to 13.52% day^{-1} at 8°C for *Pseudocalanus* sp., and from 29.65 to 15.14% body weight day^{-1} at 15.5°C and from 17.86 to 9.54% day^{-1} at 8°C for *P. elongatus*Th.

The results in this study indicate that in general the growth rate of *Pseudocalanus* sp. for developmental stages CII–CV increased with rising temperature. However, when the phytoplankton concentration was lower than the food concentration required for maximum growth, the growth rate was not correlated with temperature. For example, with a limited food supply, g was inversely related to temperature at $Phyt < 50$ mg C m^{-3} for stage CII and at $Phyt < 100$ mg C m^{-3} for stage CV, but temperature clearly had no effect on g at $50 < Phyt < 75$ mg C m^{-3} for stage CII and $100 < Phyt < 200$ mg C m^{-3} for stage CV. This suggestion was given by Vidal (Vidal, 1980a) for *Pseudocalanus* sp. (see figure 8 in Vidal's paper).

Stage duration

The computed results show that the minimum stage duration, $D_{\min}$, for *Pseudocalanus* sp. as well as for *P. elongatus*Th after Thompson (Thompson, 1982) increased with falling temperature. For the early stages (CII, CIII and CIV), $D_{\min}$ for *P. elongatus*Th was similar at different temperatures; however, $D_{\min}$ of *P. elongatus*Th fell with increasing stage of development. But for the larger stage CV, $D_{\min}$ for *P. elongatus*Th was higher than $D_{\min}$ for the smaller stages at all temperatures, and for *Pseudocalanus* sp. it was higher only at high temperatures (see Figure 3). The minimum total stage duration, $TD_{\min}$, for stages from CII to CV was similar for these two species at temperatures from 8 to 15.5°C. For example, for *Pseudocalanus* sp., $TD_{\min}$ was 9.68 days at 15°C and 14.95 days at 8.6°C, but for *P. elongatus*Th, $TD_{\min}$ was 9.62 days at 15°C and 15.78 days at 8.6°C. A slight difference in $TD_{\min}$ was also found between the two species. At high temperatures, it was <0.1 day, but at lower temperatures it was ~1 day (see the inset in Figure 3).

Figure 4 provides comprehensive information on the effects of interactions between temperature and developmental stage on stage duration in *Pseudocalanus* sp. The results indicate that the average time to reach each stage D decreased with increasing food concentration to the minimum stage duration, $D_{\min}$, at all temperatures. At low food concentrations ($10 \leq Phyt < 50$ mg C m^{-3} for CII, CIII and CIV; $10 \leq Phyt < 100$ mg C m^{-3} for CV), D increased with rising temperature in the 8–15.5°C range; this is a novel result for *Pseudocalanus* sp., obtained only through numerical calculations, and has not yet been verified by experimental data [see figure 2 in Vidal (Vidal, 1980a)]. At higher food concentrations ($Phyt > 100$ mg C m^{-3} for CII, CIII and CIV; $Phyt > 250$ mg C m^{-3} for CV), D was inversely related to temperature (Vidal, 1980a; Thompson, 1982; Klein Breteler *et al.*, 1995). However, when the food concentration lay in the range $50 < Phyt < 100$ mg C m^{-3} for stages CII–CIV and $100 < Phyt < 250$ mg C m^{-3} for CV, the effect of temperature on D could not be assessed from these data. As Figure 4 shows, when food concentration was low ($Phyt = 10$ mg C m^{-3}), D was higher at 15.5°C ($D_{CV} \cong 15.6$ days, $D_{CIV} \cong 9.3$ days, $D_{CIII} \cong 10.2$ days and $D_{CII} \cong 10.9$ days) than at 8°C ($D_{CV} \cong 6.9$ days, $D_{CIV} \cong 6.2$ days, $D_{CIII} \cong 6.8$ days and $D_{CII} \cong 7.7$ days). The influence of temperature and food concentration on TD for each stage duration was similar, as described above.

The calculations show that for the growth period from CII to CV, when food is in excess, *Pseudocalanus* sp. live longer at lower than at higher temperatures. The total stage duration CII–CV is ~36 days at 15.5°C and 27 days at 8°C when the population is starving ($Phyt = 10$ mg C m^{-3}); however, it is ~9.7 days at 15.5°C and 16 days at 8°C as the food concentration rises to high values, at which the growth rate tends to become constant ($Phyt = 300$ mg C m^{-3}). Hence, at low temperatures and food concentrations ($T = 8$°C, $Phyt = 10$ mg C m^{-3}), the individual only reaches maturity after some considerable time (~67 days, assuming that the duration of the copepodid stages makes up ~40% of the total development time); however, at high temperatures and high food concentrations (T = 15.5°C, $Phyt$ = 300 mg C m^{-3}), it can reach maturity after just 20 days (assuming that the duration of the copepodid stages makes up ~50% of the total development time). In the present work, the average time to reach each stage refers to the mean body weight determining the development stage.

Figure 6 clearly shows the effects of interactions between temperature and food concentration on the total stage duration of *P. elongatus*^{KB} for the last four copepodid stages according to the data given by Klein Breteler *et al.* (Klein Breteler *et al.*, 1995). The changes occurring in the total stage duration TD with variations in temperature and food concentration were more pronounced at low temperatures (<10°C) and low food levels. The curves run almost parallel and there were only small differences between the curves at the higher food levels. Similar findings were obtained in the experiments with *Temora longicornis*, *Acartia clausii* and *P. elongatus* (Klein Breteler *et al.*, 1982, 1995). The present results were similar to the mean TD given by Klein Breteler *et al.* (Klein Breteler *et al.*, 1995) in the studied range of temperatures and food concentrations.

DISCUSSION

Several interactions of broad biological and ecological significance were obtained in the present study. The author has made an attempt to formulate some general statements about growth processes in *Pseudocalanus* spp. by integrating the experimental data in Vidal (Vidal, 1980a,b) with those in other papers (Paffenhöfer and Harris, 1976; Thompson, 1982; Landry, 1983; McLaren *et al.*, 1989; Klein Breteler *et al.*, 1995; Koski *et al.*, 1998).

Growth rate

An important interaction is the one resulting from the effects of temperature and food concentration on the growth rate. The growth rates of *Pseudocalanus* sp. for stages CII–CV computed here were similar to the experimental data given by Vidal (Vidal, 1980a) at all temperatures. For the smallest-sized *Pseudocalanus* sp. and *P. elongatus*Th, $g_{\max}$ increased rapidly with rising temperature, but with advancing stage of development, the effect of temperature decreased, and the larger copepods attained similar $g_{\max}$ values regardless of temperature.

A similar effect of temperature on the maximum growth rate was observed in *C. pacificus* and other species of aquatic organisms, as shown in figure 9 in Vidal's paper (Vidal, 1980a) for a marine amphipod, a freshwater snail, a chaetognath and an insect larva cultured with abundant food at various temperatures. Although similar growth patterns were found for *Pseudocalanus* sp. (in this work) and *C. pacificus* (Vidal, 1980a), their growth rates, on a developmental stage basis, differed considerably. For early stages, g was considerably lower for *Pseudocalanus* sp. than for *C. pacificus* [Figure 2 in this paper and figure 7 in Vidal's paper (Vidal, 1980a)], and the difference in g between the two species was more pronounced at the highest temperatures. For example, for stage CII at 15.5°C, $g_{\max}$ was 26.45% day^{-1} for *Pseudocalanus* sp. and 41.25% day^{-1} for *C. pacificus*; but at 8°C, $g_{\max}$ was 15.82% day^{-1} for *Pseudocalanus* sp. and 18.79% day^{-1} for *C. pacificus*. With advancing stage of development, the difference in $g_{\max}$ between the species decreased, and for the later stages $g_{\max}$ was similar and even slightly higher for *Pseudocalanus* sp. than for *C. pacificus*.

Differences in $g_{\max}$ were found between *Pseudocalanus* sp. and *P. elongatus*Th. The variability range of $g_{\max}$ for *P. elongatus*Th was larger than for *Pseudocalanus* sp. (Table I; Figures 1 and 2). These differences were caused by the fact that: (i) two species of *Pseudocalanus* were considered; (ii) the materials were collected at stations in two different regions; (iii) the food composition was different; and (iv) the quantitative expression describing $g_{\max}$ of *Pseudocalanus* sp. was obtained with original experimental data; however, the development time of *P. elongatus*Th at the high food concentrations given by Thompson (Thompson, 1982) was used to obtain $g_{\max}$. These slight differences suggest that the total duration of stages CII–CV is similar in these two species over the studied range of temperatures, as the present work has shown.

On the basis of material collected in the Gulf of Gdansk (Baltic Sea), Ciszewski and Witek (Ciszewski and Witek, 1977) and Witek (Witek, 1995) calculated the growth rate of *P. elongatus*. The main food source was provided by *Kirchneviella obesa*, *Microcystis aemginosa*, *Euglena* sp., *Navicula* sp. and *Gymnodinium* sp. The growth rate of *P. elongatus* calculated by Ciszewski and Witek (Ciszewski and Witek, 1977) was 5.8 for CII, 4.1 for CIII, 3.4 for CIV, 2.6 for CV and 0.8% of body weight day^{-1} for adults at 5°C. According to these findings, it appears that $g_{\max}$ of *P. elongatus* from the Baltic Sea (Gdańsk Deep) at 5°C is about half that of *P. elongatus* from the North Sea for small copepods, but is about three times lower for the largest ones. The significant difference in g between the two species is mainly the result of the low salinity in the Baltic Sea. *Pseudocalanus elongatus* is quite euryhaline or properly marine euryhaline, 4–5 p.s.u. appearing to be the lowest tolerable salinity (Kinne, 1963). The biomass of *P. elongatus* from the Baltic Sea is largely dependent on salinity (Möllmann *et al.*, 2000) and decreases with diminishing salinity.

Stage duration

The results in this paper indicate that the average time to reach a given stage became shorter as the ambient temperature increased with food concentrations higher than $Phyt_c$ for each stage, but at lower phytoplankton concentrations, temperature clearly had no effect on D. Values of D computed here for *Pseudocalanus* sp. are similar to the original results given by Vidal (Vidal, 1980a) at much the same range of temperature and of food concentration, except for $Phyt < 50$ mg C m^{-3}, where the D values for the particular stages were a little higher at all temperatures.

The results of TD for *P. elongatus*^{KB} obtained here are similar to the experimental data given by Klein Breteler *et al.* (Klein Breteler *et al.*, 1995). These values are ~3 days shorter than for *P. elongatus*Th and *Pseudocalanus* sp. in the presence of excess food in the range of temperatures studied (Figure 7). The difference in TD is caused by the fact that the food source in these cases was different. The results of the present study also demonstrate that TD of *Pseudocalanus* sp. rose with decreasing temperature in the studied range of food concentration, except that at food concentrations in the range $50 < Phyt < 100$ mg C m^{-3}, temperature clearly had no effect on TD for *Pseudocalanus* sp.

The influence of different phytoplankton concentrations on generation times from hatching to the adult form of *P. elongatus* was also studied in laboratory cultures at 12.5°C by Paffenhöfer and Harris (Paffenhöfer and Harris, 1976), where *Thalassiosira rotula* was the food source. The total duration for stages CII to 50% adult ranged from 12.5 to 15.5 days and was similar at different food concentrations, with the exception of the lowest concentration, 25 mg C m^{-3}, where the total duration was 18.5 days. The average time for stages CII to 50% adult for all experiments was 14 days at 12.5°C. However, in the present work, the average time obtained was 16.8 days at 12.5°C. This difference was due principally to the fact that, at low food concentrations ($Phyt$ = 25 mg C m^{-3}), the total duration for stages CII–CV of *Pseudocalanus* sp. was 25 days, i.e. it was higher than for *P. elongatus*; however, at higher $Phyt$ it was similar.

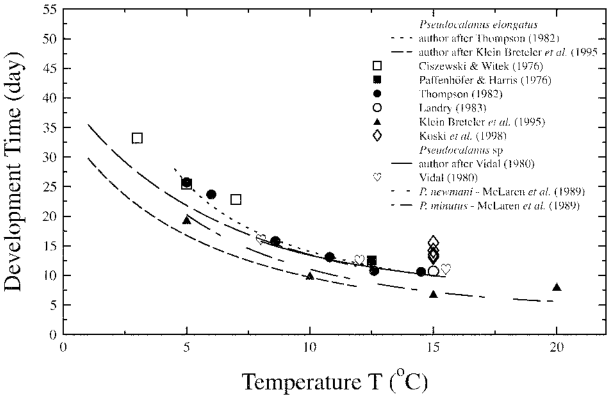

Fig. 7. *Pseudocalanus* spp. Relationships between development times TD (in days) for stages CII–CV and temperature T (in °C) when excess food is available.

The total stage duration CII–CV for *P. elongatus* from the southern Baltic Sea given by Ciszewski and Witek (Ciszewski and Witek, 1977) was 33.2 days at 3°C, 25.4 days at 5°C and 22.8 days at 7°C (see Figure 7). The development time for stages CII–CV at 5°C is similar to the results in this paper for *P. elongatus*Th from the North Sea (Thompson, 1982). However, at temperatures >5°C, it is shorter (~4 days at 7°C); below this temperature, it is longer (~5 days at 3°C) (Figure 7).

Landry determined the development times of seven species of planktonic marine copepods from the waters of southern California or Puget Sound at 15°C and excess food (Landry, 1983). The duration of the copepodid stages represents 53.5, 50.8, 45.8, 47.9, 60.6, 57.3 and 61.6% of the generation time (18.6, 21.1, 21, 20.3, 34, 25.4 and 19.8 days) for *Paracalanus parvus*, *Pseudocalanus* sp., *A. clausii*, *Acartia tonsa*, *Labidocera trispinosa*, *Rhincalanus nasutus* and *C. pacificus*, respectively. The duration of the copepodid stages from this study was 9.95, 10.7, 9.6, 9.7, 20.6, 14.6 and 12.2 days, respectively.

McLaren *et al.* studied the development time of four eastern Canadian species separately at temperatures between 0 and 12°C at an excess supply of food consisting of a mixture of algae (McLaren *et al.*, 1989). The Belehrádek curves he calculated for *Pseudocalanus minutus* and *Pseudocalanus newmani* run parallel to the curves for *Pseudocalanus* sp. for stages CII–CV at the high food concentrations and at temperatures >8°C (Figure 7). However, below this temperature, the curves increase less steeply than for *P. elongatus*, resulting in a total stage duration CII–CV of ~7 days for *P. minutus* and 12 days for *P. newmani* at 4°C. Figure 7 also indicates that the development time for stages CII–CV for *P. minutus* (McLaren *et al.*, 1989) is nearly equal to the present results for *Pseudocalanus* sp. [a species resembling *P. minutus*; see Vidal (Vidal, 1980a)] obtained here at temperatures >8°C.

Large differences in development times were obtained by Koski *et al.* at 15°C with different species of algae (Koski *et al.*, 1998). Development was fastest with *Rhodomonas* sp., *Thalassiosira weissflogii* and *Gymnodinium simplex*. With these species, *P. elongatus* was able to complete its development in 22–25 days (13.5–15.4 days for the period from CI to CV, see Figure 7), which is slightly slower than the value found in this paper and previous studies (Paffenhöfer and Harris, 1976; Vidal, 1980a,b; Thompson, 1982; Landry, 1983; Klein Breteler *et al.*, 1995).

On the basis of the findings in this work, the total duration for stages CII–CV of *Pseudocalanus* sp. was 9.7 days and for *P. elongatus* 9.6 days according to the data in Thompson (Thompson, 1982) and 6.7 days after the data given by Klein Breteler *et al*. (Klein Breteler *et al*., 1995) at 15°C and at excess food, which are generally comparable to the literature values (Vidal, 1980a,b; Thompson, 1982; Landry, 1983; McLaren, 1989; Klein Breteler *et al*., 1995).

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